

**LIFE HISTORY OF *PTEROMALUS COLORADENSIS* (ASHMEAD)
(HYMENOPTERA: PTEROMALIDAE) A PARASITE OF
PARACANTHA GENTILIS HERING (DIPTERA: TEPHRITIDAE) IN
CIRSIIUM THISTLE CAPITULA**

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Abstract.—The biology and behavior of *Pteromalus coloradensis*, a solitary larval-pupal parasite of *Paracantha gentilis*, a thistle-capitulum-infesting tephritid, are described. *Pteromalus coloradensis*, previously known from a single female collected in Colorado, is reported herein from California. We describe larval and pupal development using laboratory reared specimens, and oviposition, feeding, and reproduction from field and laboratory observations. Scanning Electron Microscopy of adult mandibles was used to determine the function of the dentition during emergence from the host puparium and overwintered capitula. Morphometric analysis of individual host puparia and parasites showed three distinct relationships between size and sex of the parasite to the size of the host puparium, substantiating predetermination of sex by the ovipositing female. Courtship behavior and the side mounting of the female by the male during copulation have not been previously described for males in *Pteromalus*. A description of the male is given.

Key Words: Insecta, *Paracantha*, *Cirsium*, *Pteromalus*, parasite, functional morphology, courtship behavior

This study of *Pteromalus coloradensis* (Ashmead) was undertaken while working on the life history of its host, *Paracantha gentilis* Hering, a stenophagous capitulum-infesting tephritid on *Cirsium* thistle species in western North America (Foote and Blanc 1963, Goeden and Ricker 1986a, b, 1987a, b). Ashmead (1890) described *Pteromalus* (= *Rhopalicus*) *coloradensis* from one female specimen taken at West Cliff, Colorado; no rearing records were given. Rare is the opportunity to describe the life history of a parasite, but *Pt. coloradensis* lent itself well to study, thus we were able to obtain as complete a record of its biology and behavior as known for any other North American species in this family.

MATERIALS AND METHODS

Cirsium californicum Gray capitula containing host puparia were collected from Mill Creek, San Bernardino National Forest, San Bernardino Co., California, 16 km N.E. of Mentone, and *Cirsium proteanum* J. T. Howell capitula were collected from Sawmill Mt., Angeles National Forest, Los Angeles Co., California, 25 km S.E. of Gorman, during the Spring and Summer of 1987 and 1988 (Headrick and Goeden 1990). The capitula were dissected to remove the host puparia which were then individually placed in 60-ml clear plastic rearing vials. Newly emerged adults of *Pt. coloradensis* were maintained on a diet of honey which was streaked onto the inside of the vials. Cou-

ples, consisting of virginal males and females, were placed together in a vial to observe courtship and copulatory behavior. The larvae and pupae were placed onto moistened filter paper in covered glass petri dishes and held in darkened growth chambers at 27°C to determine developmental rates.

Specimens for Scanning Electron Microscopy were killed by freezing, then either air-dried or fixed in osmium tetroxide for 24 h (Sabatini et al. 1963), and finally placed on stubs and sputter-coated with a gold-platinum alloy. The SEM used was a JOEL-JSM-35C3 in the Department of Nematology, University of California, Riverside. Specimens were examined and micrographs prepared at 15 kV accelerating voltage on Polaroid 55 P/N film. All micrograph negatives are stored with Gordon Gordh, Department of Entomology, University of California, Riverside. Voucher specimens of *Pteromalus coloradensis* from this study are deposited in the research collection of RDG and the United States National Museum of Natural History for incorporation into the Chalcidoidea collection.

RESULTS

Biology.—New California records. San Bernardino Co.: Mill Creek, 16 km N.E. of Mentone on State Hwy. 38, San Bernardino Nat. Forest, 14 F, 16 M, ex. *Pa. gentilis* on *C. californicum* 25-IV-87 to 14-VI-88 (D. Headrick, UCR). Los Angeles Co.: Sawmill Mt., 25 km S.E. of Gorman at Sawmill campground, Angeles Nat. Forest, 10 F, 5 M, ex. *Pa. gentilis* on *C. proteanum* 29-VII-87 (D. Headrick, UCR).

Immature stages.—*Pteromalus coloradensis* is a solitary, larval-pupal endoparasitoid. The egg is laid within the host during the larval stages, but the host continues its development through pupariation. Dissections revealed that parasite larvae completely consumed the pupa within the puparium only after the completion of pupariation. However, three (5%) of 60 pu-

paria taken from post-blossom capitula of *Cirsium proteanum* contained parasite larvae that fed on the late pupal stage of the host, leaving an empty, unemerged host pupa inside the puparium. Normally, however, the overwintered larva consumed the entire contents of the host and used the hollowed puparium for its own pupation.

The last instar larva pupated with its head directed anteriorly inside the host puparium beginning in February in both the field and the laboratory. Pupal development lasted 3 to 4 days under insectary conditions. Four partly opened host puparia containing last-instar parasite larvae were held in darkened growth chambers and observed every 12 h during pupation. Within the first 24 h, the larva developed into an opaque white pupa resembling the size and shape of the adult and which could be sexed (there were three males and one female). After 36 h, the head and mesosoma became iridescent green while the metasoma distad of the propodeum remained white. After 60 h, the male metasoma had completely turned an iridescent green; however, the female sterna remained unpigmented and the gonopore and unsclerotized ovipositor could be seen rhythmically pumping ca. once per second. The antennae and legs of individuals of both sexes were observed moving within the confines of the pupal integument. After 72 h, the female's first-four sterna distad from the propodeum became an iridescent green, and the ovipositor was sclerotized to a golden color. The antennae and legs moved more rapidly than previously was observed and showed twisting movements, the mesosoma swelled every 5 to 10 min. The males emerged before 84 h had elapsed and the female emerged later after 94 h.

Adult.—Host puparia ($n = 82$) dissected from capitula of *C. californicum* and *C. proteanum* were caged individually in ventilated rearing vials and held in the insectary at constant conditions; 11 (13%) parasites emerged within 1 month. From three of the puparia obtained from *C. californicum* heads

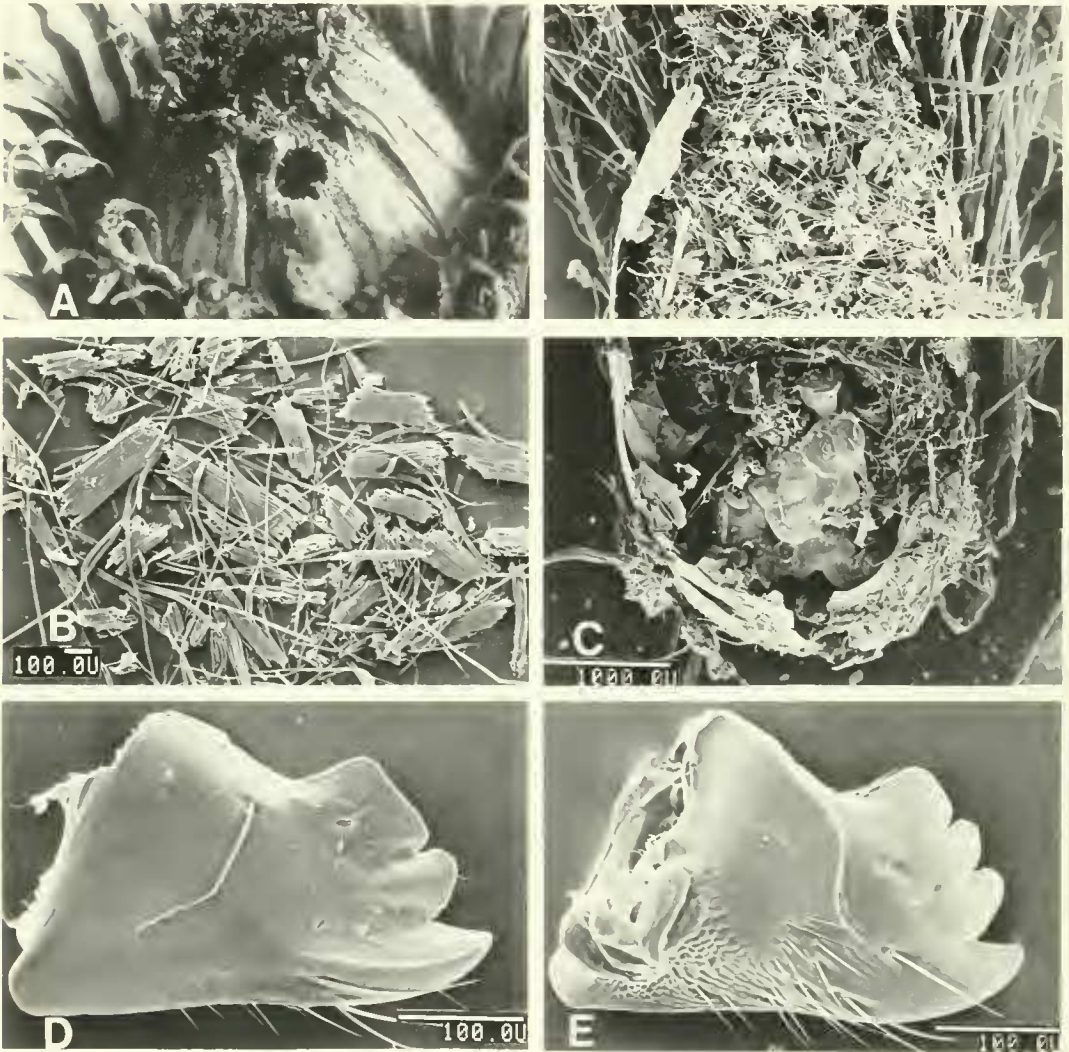


Fig. 1. (A) Emergence hole in over-wintered head of *C. californicum*. (B) Catacord. (C) Catacord in dissected host puparium. (D) Inside surface of left mandible. (E) Outside surface of right mandible.

caged on 9-VI-1987, parasites first emerged on 11-II-1988 after 8 months in the insectary. Adults emerged between 7-II to 9-III-1988, from overwintered heads collected on 3-II-1988 at the Mill Creek site. Emergence from overwintered heads in the field began on 12-III-1988. Males emerged first, and after a week, females began to appear. Field observations and laboratory rearings suggested that a portion of the first generation of the parasite population emerges in sum-

mer and parasitizes the last of the current host generation. The remainder of the first generation as well as this second generation of parasites overwinters in puparia within closed capitula and presumably emerges the following spring.

Adults exit the host puparium by chewing a small, circular hole near the anterior end, but never at the apex. They exit the capitulum by chewing a tunnel through the dried floral tubes, pappus and bracts of the over-

wintered head (Fig. 1A). As the emerging parasite adult progresses through the head, the chewed material, here given the name "catacord" (Fig. 1B), is systematically packed into the empty puparium (Fig. 1C).

The mandibular structure was viewed with the SEM to determine the method of excision and cutting of the catacord. In this genus there can be a difference in dentition between left and right mandibles, e.g. in *Pt. coloradensis* the right has four teeth and the left has three teeth in both sexes (Fig. 1D, 1E). The dorsal tooth has a broad, chisel shape and a sharp leading edge. The left dorsal tooth is twice as broad as the right. The middle teeth are rounded with sharp leading edges. Both mandibles have a ventral tooth which is elongate, conical and tapers to a point apically. The emerging parasite faced two very different substrates through which it had to chew. The first obstacle was the puparium which was hard, concave, and without much surface texture (Headrick and Goeden 1990). The two ventral teeth punctured the wall of the puparium and then were brought together to make a cut. The parasite continued to cut a circular hole, until eventually the excised piece of shell was freed, then pushed down into the bottom of the puparium. The next obstacle was the dried capitulum tissues consisting of floral tubes and compact fibers of pappus. As the parasite exited the puparium, it chewed through the capitulum at an angle perpendicular to the fibers. By lifting its head, the plane of the cutting teeth was in a position to grasp and cut through the fibers. The uniform width of the catacord is thus defined by the limit of mandible extension and the tunnel diameter is a function of the degree of rotation of its head.

Orientation of exit holes in capitula lying on the ground, remaining on upright plants or in rearing vials was always the same regardless of the positions of the capitula (Fig. 1A). Capitula stored in darkened rooms over the winter and later dissected showed that most parasites had tunneled within the head

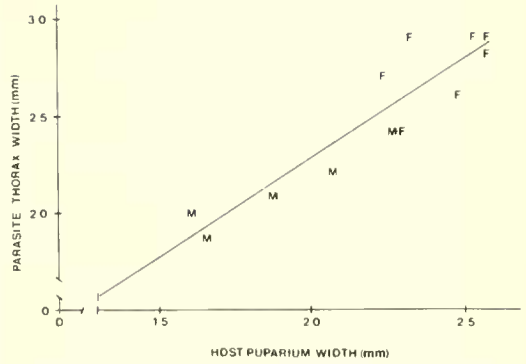


Fig. 2. The relationships of the parasite thorax width at its widest point and the host puparium width at its widest point. F, female; M, male; (central M F, represents a shared data point).

in various directions but did not exit. Thus, perception of increasing light intensity may help guide successful emergence from a capitulum.

Three relationships between the maximum width of the parasite thorax and the maximum width of the host puparium from which the parasite emerged are diagrammed (Fig. 2). There is a distinct separation between size and sex in the parasite, i.e. females are larger than males. There is a separation, with little overlap, between the sex of the parasite and the host size. There is a significant correlation (corr. coeff. = 0.926, $P = 0.0001$) between parasite size and host size. These relationships indicate that host size, or available resource, is a significant factor in determining the sex and size of the parasite. We hypothesize evidence of selective oviposition by parasites based on host sex, i.e. female parasites will lay fertilized (or female) eggs into female hosts, and unfertilized (or male) eggs into male hosts (Crozier 1971, Slobodchikoff and Daly 1971, Charnov 1982).

Behavior.—*Hostfinding*: *Cirsium* thistle capitula that are infested do not shed achenes and remain closed and overwinter on or near the parent plant. The parasitized tephritid puparia inside these heads are insulated by the dried achenes and pappus against freez-

ing winter temperatures. These overwintering heads, from which adults of *Pt. coloradensis* emerge in spring, are scattered among the current season's thistle plants, thereby facilitating host finding by newly emerged parasites.

Males and females were observed to fly directly to and land on the capitula of thistles where they apparently searched for food, mates, and oviposition sites. Usually, neither sex was observed on other parts of the thistles, but occasionally males were observed to land on the upper surfaces of leaves. Adults also were observed resting on the leaves of nearby plants other than thistles, but were not observed feeding, mating or ovipositing on these plants. The peak activity period for *Pt. coloradensis* was from 1000 to 1500 h. They did not remain on the thistles overnight, but were observed to fly to them each morning.

Feeding: On three occasions individual males and females were observed feeding on the exudate from *Paracantha gentilis* oviposition wounds.

Oviposition: Females search the surface of a head by antennating in an apparently random manner. In selecting an oviposition site, the female places her mouthparts on the surface, moves away, then returns and touches her mouthparts again to the same site. The number of these return visits varied from two to five. Then, positioning herself head-up on the capitulum over the site just selected, she places the apex of her metasoma on the outer surface of the bract, planting the ovipositor tip so that she can unhinge the ovipositor by stepping backwards. She continues stepping backwards until the ovipositor is perpendicular to the long axis of her body and to the outer surface of the capitulum. This allows her to balance upon the ovipositor and to pull herself downward with her legs. Drilling begins with a slight twist of the metasoma in a lateral plane and a side-to-side rocking of the body. By continuing to pull downward she pushes the ovipositor through the bracts and finally into the softer tissues of the capitulum.

Once the hole is drilled and the female has the ovipositor inserted completely into the head, she pushes with her legs in a slight up-and-down motion, presumably searching for a host larva. If none is found, she then uses her legs to push up and away from the capitulum surface to remove the ovipositor. Once removed, it is secured by stepping forward. Females were first observed to oviposit in thistle capitula in late March. They select young capitula that are fully exposed, or at least free from surrounding leaves. Apparently, *Pt. coloradensis* females do not distinguish capitula infested by *Pa. gentilis*, because early in the season they drill into uninfested capitula. This indicates that they failed to associate the oviposition wounds of *Pa. gentilis* in capitula at which the parasite adults fed with the presence of host larvae. The time spent on a capitulum by a female parasite varied from 1 min to 2.5 h. Females were observed to drill from one to six holes during observation periods that lasted a maximum of 2.5 h. The average time spent in drilling holes was 8 ± 2 ($\bar{x} \pm \text{SE}$) (range, 2–22, $n = 13$) min; the average time between drillings was 8 ± 2 (range, 1–15, $n = 7$) min. Dissections showed that if no host was located inside a capitulum, or only host eggs were present, no parasite egg was deposited. Capitula dissected after oviposition showed that drill holes occurred in rows along the vertical axis of the capitulum, from about one-third the distance between the apex of the capitulum to the peduncle. On three separate occasions females were observed drilling into the undersides of capitula near the peduncle. Five capitula collected 3 weeks after the first observation of parasite oviposition contained on average of 36 ± 5 (range, 20–49) drill holes.

Courtship.—*Laboratory:* Two each, newly emerged (<48 h old) virgin males and females were caged as couples (one male and one female) in separate screened plastic vials for ca. 30 min observation, after which they were separated. Courtship behavior began an average of 15 ± 4 (range, 5 to 30) min after caging ($n = 9$). Males approached fe-

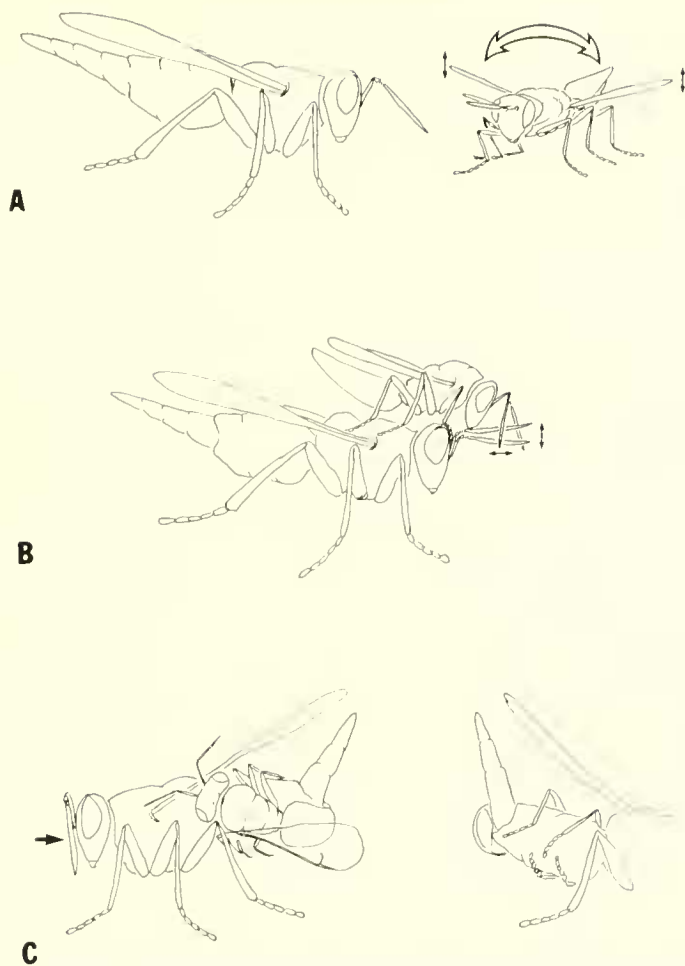


Fig. 3. (A) Male initiating courtship: dual-directional arrows indicate wing fanning and lateral weaving. (B) Antennation posture: dual-directional arrows indicate antennal movement. (C) Position of male and female in copula viewed from both sides. Arrow shows depressed antennae in female. Male drawn with right pair of wings removed.

males either laterally or head-on and stopped when they were 1 cm or less apart, but not touching. With his antennae extended, the male began to sway his body from side to side and fan his wings (Fig. 3A). Swaying consisted of a lateral rocking motion, while moving his body over his legs from one side to the other.

Wing fanning as a form of auditory courtship communication has been described for two other pteromalids, *Pteromalus puparum* L. and *Nasonia vitripennis* (Walker) (Miller and Tsao 1974). Experimentation

has shown that males vibrate their wings at a specific frequency and pulse which is then followed by the male mounting the female. Wing fanning by *Pt. coloradensis* males also preceded their mounting of the females and beginning antennation.

Antennation occurred while the male stood on the female's dorsum with his foretarsi on the vertex of her head, his middle tarsi in front of her tegulae, and his hind tarsi grasping her axillae (Fig. 3B). The female drummed the upper surface of her funicle segments 1–3 against the closed man-

dibles of the male. This is in contrast to the courtship behavior described for other Pteromalidae, e.g. *Nasonia* and *Eupteromalus* (cf. Barass 1960, van den Assem 1974), where males moved their open mandibles over the upper surface of the female's funicle segments. While the female of *Pt. coloradensis* drummed her antennae on the mouthparts of the male, he intermittently stroked the lateral aspects of her antennae with his funicular segments (Fig. 3B), as is common in the Pteromalinae (van den Assem 1974). Single antenation episodes lasted an average of 3 ± 0.4 s (range, 1–5 s, $n = 12$). When the female was receptive, only one such episode occurred before copulation and was of short duration, i.e. ca. 2 s. If the female was unreceptive, yet still confined with the male in the vial, antenation occurred up to seven times during a 30-min period, including five times in a 10-min period, each episode terminating with the male dismounting. The intervals between male approaches varied from 1 to 30 min.

Mating.—*Laboratory*: If the female was receptive after antenation, she lowered her flagella and held them tightly against her head, a motion that has been reported to be the receptivity signal to the male (Barass 1960, van den Assem 1974), and simultaneously, raised the apical four segments of her metasoma to expose the gonopore. The male immediately moved backwards and down her left side, bent his metasoma down and under her metasoma, and placed the apex on the gonopore (Fig. 3C). This copulatory position is unusual for Pteromalinae males, which usually tend to copulate from a position behind and underneath the metasoma of the female (van den Assem 1974). The female terminated the mating by relaxing her metasoma and "shaking-off" the male. Two matings lasted ca. 30 s each. No post-copulatory behavior was observed. The male did not try to remount the female, but both actively moved inside the vial for the duration of the observation time.

Field: One courtship and copulation sequence was observed on the apex of a *C. californicum* terminal capitulum. The male approached the female and began swaying and wing fanning for ca. 2 s. He then mounted her for antenation as described above for ca. 3 s. Copulation followed and lasted about 1 min. Males were observed to approach, mount, antennate, and dismount any female they contacted. On separate occasions, three different males mounted and antennated a single female as she was ovipositing.

DISCUSSION

Zwölfer (1988) discussed biogeography of thistles and suggested that they crossed into North America from the Palearctic prior to the late Miocene via the Bering Strait. Few of the associated Palearctic insect taxa followed their *Cirsium* host plants, and few insect taxa of true Nearctic origin use them for host plants. The genus *Paracantha*, however, is an exception (Goeden and Ricker 1986b, 1987a, b, Zwölfer 1988), being originally Nearctic. *Pteromalus coloradensis* may have followed its host onto *Cirsium*, having been pre-adapted, with an elongate ovipositor, to parasitizing *Pa. gentilis* in other capitula. Such an adaptation may also have resulted in the unique copulatory position of the male having to move to the side of the metasoma of the female.

The thistle-insect complexes that have been studied in the Palearctic (Zwölfer 1985, 1988) have phytophagous arthropod guilds that are in turn attacked by guilds of parasites. In southern California, there is a paucity of phytophagous species on thistles compared to the fauna of Europe (Zwölfer 1965, Goeden and Ricker 1986a, b, 1987a, b), and parasite species attacking them also are few. No other species of *Pteromalus* in North America is known to attack tephritid hosts (Krombein et al. 1978).

Information on host relationships for *Pteromalus* in North America may not give as clear an indication of generic relation-

ships as that of European species. *Pteromalus coloradensis* was placed in the genus *Habrocytus* until *Pteromalus* and *Habrocytus* were synonymized by Bouček and Graham (1978). In Graham's (1969) discussion of the Pteromalidae of North-West Europe, 67 *Habrocytus* species were included, of which 35 (52%) had unknown biologies. Of the 32 species whose biologies were known, 14 (43%) were parasites of Tephritidae exclusively, and the other 18 species parasitized various phytophagous Lepidoptera and Coleoptera. The Tephritidae hosts listed in Graham (1969) are non-frugivorous species infesting capitula of various Asteraceae, mainly belonging to genera in the tribe Cardueae (thistles and knapweeds), e.g. *Centaurea*, *Cirsium* and *Carduus*. Two of the Lepidoptera and Coleoptera hosts listed were also associated with Cardueae. Of the nine *Pteromalus* species included, none were listed as parasites of Diptera. When Bouček and Graham (1978) transferred *Habrocytus* to *Pteromalus*, they invalidated the generic significance of such host relationships. Data on the biologies of a host and parasite are never complete, and often not useful in taxonomy; however, when biological information is available, such as that listed by Graham (1969), it could help to clarify taxonomic questions.

DESCRIPTION OF THE MALE

Unknown until this study, the male of *Pt. coloradensis* is described here. Body iridescent blue-green, head and thorax coarsely reticulate and tinged with gold, metasoma smooth and tinged with copper. Antenna mostly fuscous; scape, pedicel smooth and testaceous; flagellum fuscous. Coxae concolorous with thorax; trochanters testaceous; femora concolorous with coxae except apices testaceous; tibiae completely testaceous; tarsi testaceous proximally, fuscous distally. Tegulae testaceous. Wings hyaline, venation testaceous.

Head (Fig. 4A).—Head as broad as meso-scutum, coarsely reticulate, eyes separated

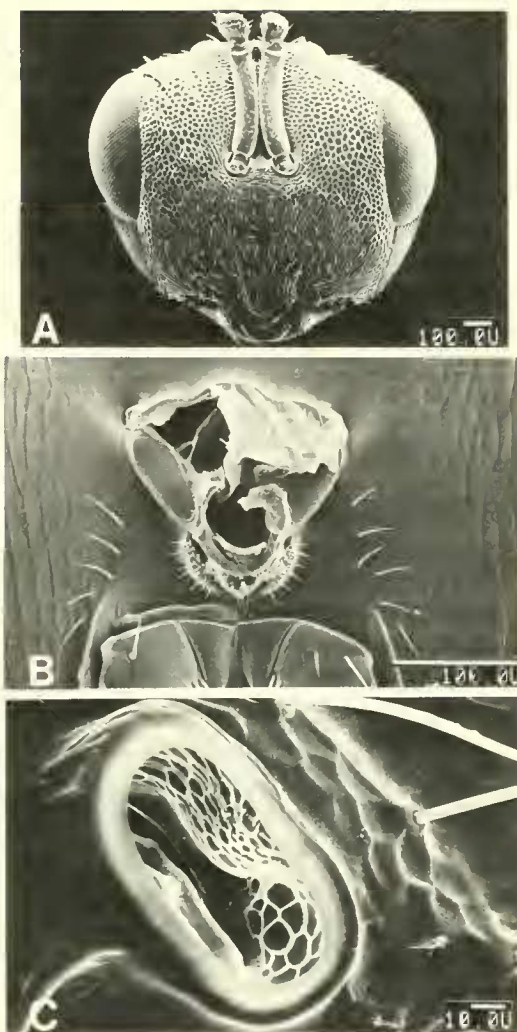


Fig. 4. (A) Anterior view of the male head. (B) Posterior view of the male head. (C) Thoracic spiracle of the male.

dorsally by $1.5 \times$ their length; malar space nearly $\frac{1}{2} \times$ eye height; clypeus striate, anterior margin cleft medially. Antenna inserted $\frac{1}{3}$ above lower ocular line, scape length ca. $\frac{3}{4}$ eye length, nearly reaching lower edge of median ocellus; combined length of pedicel and flagellum $1.1 \times$ head width; pedicel width $1.5 \times$ length, about $\frac{1}{2}$ length of first funicular segment; funicle segments quadrate, stouter than pedicel; clavus length not quite twice width, slightly longer than combined length of preceding two funicular

segments; sensilla numerous, usually in one row circumscribing funicle segment. Posterior aspect of head with many longitudinal furrows; setae sparse, a row of up to six setae on either side of occipital foramen extending from the ventral edge of the posterior tentorial bridge to the dorsal edge of the maxillary insertion, occipital foramen triangular, as wide as maxilla at insertion (Fig. 4B).

Pronotal collar sharply margined anteriorad. Propodeum width $1.8 \times$ scutellar width; $3 \times$ length; plica distinctly bordered by fine reticulation; panels shiny with longitudinal coarse wrinkles; costula distinct as a lateral band of reticulation between apical foveae; median carina absent; nucha with small wrinkles and a band of coarse reticulation at base. Spiracles elongate-oval set at ca. 45° angle to midline, inner walls with distinct reticulation (Fig. 4C).

Forewing with costal cell bare; speculum open below, extending $\frac{1}{2}$ way below marginal vein; stigmal vein with one row of setae, and $1.1 \times$ longer than marginal vein and slightly longer than the postmarginal vein.

Gaster elongate-oval, length $2.2 \times$ width, dorsally compressed and with a flat dorsal surface, ventral plica; narrower than thorax; basal tergum occupying $\frac{1}{3}$ of total length.

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